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Brian L. Cypher
EG&G Energy Measurements, Inc.
P.O. Box 127
Tupman, CA 93276
805-763-6140

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INFLUENCE OF PHYSIOGRAPHY AND VEGETATION ON SMALL MAMMALS AT THE
NAVAL PETROLEUM RESERVES, CALIFORNIA

BRIAN L. CYPHER, EG&G Energy Measurements, Inc., P.O. Box 127,
Tupman, CA 93276

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Abstract: Influence of physiography and vegetation on small mammal abundance and species composition was investigated at Naval Petroleum Reserve No. 1 in California to assess prey abundance for Federally endangered San Joaquin kit foxes (Vulpes macrotis mutica) and to assess the distribution of two Federal candidate species, San Joaquin antelope squirrels (Ammospermophilus nelsoni) and short-nosed kangaroo rats (Dipodomys nitratoideus brevinasus). Live-trapping and vegetation sampling were conducted at 20 sites evenly distributed among four physiographic regions defined by slope orientation and terrain: South-Flat, South-Hilly, North-Flat, and North-Hilly. Mean capture rate for all species combined did not differ among regions, and was not correlated with either vegetative cover or shrub density. However, number of species and species diversity differed among regions and were highest on South-Flat sites and lowest on North-Hilly sites. Abundance of kangaroo rats (Dipodomys spp.), which are important prey for kit foxes, also was similar among regions. Capture rates for San Joaquin antelope squirrels were higher on south-facing sites and were negatively correlated with vegetative cover. Capture rates for short-nosed kangaroo rats were higher in flat terrain sites.

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Key words: abundance, California, community composition, rodents, San Joaquin kit foxes, small mammals.

The influence of physiography and vegetation on small mammal abundance and species composition was investigated on Naval Petroleum Reserve No. 1 (NPR-1) in the southern San Joaquin Valley of California. Physiography influences soil attributes, such as nutrients and moisture, and these in turn influence vegetation characteristics (Brady 1974). Vegetation characteristics can influence abundance of small mammals (Brown 1975, Brown and Harney 1993).

On NPR-1, vegetation characteristics were reported to vary between north and south sides of the east-west oriented Elk Hills ridge which traverses the site (EG&G Energy Measurements, Inc. 1992b), and the effects of this variation on small mammal abundance was unknown. Abundance of Federally endangered San Joaquin kit foxes (Vulpes macrotis mutica cf. Mecure et al. 1994) also appears to vary with physiographic features, particularly terrain (EG&G Energy Measurements, Inc. unpubl. data), and such variation might be attributable to differences in the availability of prey, such as small mammals. Small mammals, particularly kangaroo rats (Dipodomys spp.), are a primary item in the diet of kit foxes on NPR-1 (Scrivner et al. 1987). In addition, two Federal candidate (Category 2) small mammals, the San Joaquin antelope squirrel (Ammospermophilus nelsoni) and the short-nosed kangaroo rat (D. nitratoides brevinasus), are present on NPR-1. The influence of physiography and vegetation on the local distribution and abundance of these two species is unknown.

The specific objectives of this investigation were to determine whether small mammal abundance and community composition varied with north-south orientation, terrain, ground cover, and

shrub density, and whether these factors influenced the distribution and abundance of San Joaquin antelope squirrels and short-nosed kangaroo rats.

STUDY AREA

NPR-1 is located approximately 40 km southwest of Bakersfield, California, and is approximately 19,120 ha in size. NPR-1 encompasses most of the Elk Hills anticlinal formation which is an east-west oriented ridge. Topography is characterized by steep-sloped hills dissected by drainages, and by gently sloping alluvial plains along the northern and southern perimeters of NPR-1. Elevations range from 88 to 473 m (Woodring et al. 1932). Soils in hilly terrain are primarily classified as Elk Hills series loams and Torriorthents, while soils in flat terrain are classified as Kimberlina series sandy loams (Soil Conservation Service 1986). Climate is characterized by hot, dry summers and cool, wet winters with frequent fog (National Oceanic and Atmospheric Administration 1992). Annual precipitation averages approximately 12 cm.

The vegetation association is classified as either Lower Sonoran Grassland (Twisselman 1967), Valley Grassland (Heady 1977), or Valley Saltbush Scrub (Holland 1986). Herbaceous vegetation consists primarily of annual grasses and forbs dominated by red brome (Bromus madritensis), slender oats (Avena barbata), Arabian grass (Schismus arabicus), red-stemmed filaree (Erodium cicutarium), and peppergrass (Lepidium spp.). Common shrubs include desert saltbush (Atriplex polycarpa), bladderpod (Isomeris arborea), and cheesebush (Hymenoclea salsola).

METHODS

Small mammal abundance was assessed by live-trapping on 20 sites distributed throughout NPR-1. Five sites were established in each of four physiographic regions defined by orientation and terrain. Site orientation was categorized as being on the north side or south side of the east-west oriented Elk Hills ridge crest. For terrain, sites were characterized as being "Hilly" ($>5^\circ$ slope) or "Flat" ($\leq 5^\circ$ slope) based on slope measurements from aerial photographs. Thus, the four physiographic regions were defined as South-Flat, South-Hilly, North-Flat, and North-Hilly. Sites categorized as "Flat" actually sloped gently to the north or south. Sites were located in areas lacking evidence of anthropogenic disturbances (e.g., roads, pipelines), and each site was traversed by one sandy-bottomed wash.

At each study site, 25 trapping stations were established at 7.5-m intervals along an east-west transect. Two Sherman live traps (8 x 9 x 33 cm) were placed at each station for a total of 50 traps per site. Traps were prebaited with a mixture of peanut butter and rolled oats for three nights prior to trapping. Trapping was conducted for five consecutive nights. During the trapping session, traps were baited in late afternoon with seed and the peanut butter/rolled oat mixture and then checked the next morning. Captured small mammals were identified to species, marked ventrally with a non-toxic marking pen, sexed, aged, weighed, and released at the capture site. A capture rate, defined as the number of individuals per 100 trap-nights, was calculated for each species and site. Mean capture rate for all species combined, kangaroo rats, San Joaquin antelope squirrels, and short-nosed kangaroo rats were compared among regions using one-way analysis of variance and Tukey's multiple comparison test (Zar 1984).

To assess small mammal species diversity, a Shannon diversity index H' was calculated for each site using the equation:

$$H' = \frac{-\sum f_i \log f_i}{n}$$

where n is the total number of individual small mammals captured on each site and f_i is the number of individuals of the i^{th} species captured on each site. Mean diversity indices were compared among regions using one-way analysis of variance and Tukey's multiple comparison test (Zar 1984).

To assess co-occurrence of species on sites, Spearman rank correlations (Zar 1984) were calculated between species using capture probabilities from individual sites. For this analysis, species other than kangaroo rats and San Joaquin antelope squirrels were grouped as "small quadrupeds".

To examine the relationship between small mammals and vegetation characteristics, vegetation sampling transects were established at each monitoring site. These transects were 200 m long, and were placed 10 m south of and parallel to each small mammal trapping transect. Vegetation on sites was sampled in August 1993. Percent ground cover was estimated by using an ocular point projection device (Reynolds and Edwards 1977). Five points were sampled at 5-m intervals along the transect for a total of 200 points per site. Shrub density was estimated by counting all shrubs (≥ 30 cm tall) in a 200-m x 1-m belt along the vegetation sampling transects. Mean percent ground cover and mean shrub density were compared among regions using one-way analysis of variance and Tukey's multiple comparison test (Zar 1984). Percent cover estimates for sites were arcsine-transformed to normalize data for statistical tests (Zar 1984). The relationship

between site-specific capture rates and vegetation characteristics was assessed using correlation analysis. This analysis was conducted for all species combined, kangaroo rats, San Joaquin antelope squirrels, and short-nosed kangaroo rats. Also, the relationship between site-specific Shannon diversity indices and vegetation characteristics was assessed using correlation analysis (Zar 1984)..

RESULTS

Mean percent ground cover differed significantly among regions ($F = 7.37$; 3,16 df; $P < 0.01$), and was highest on North-Flat sites and lowest on South-Flat sites (Table 1). South-oriented sites may receive more direct insolation resulting in drier soil conditions and lower cover. Shrub density did not differ statistically among regions ($F = 1.30$; 3,16 df; $P = 0.31$) (Table 1).

Small mammal trapping was conducted from September 27 to October 1, 1993. During the session, 718 individuals of seven species were captured 1,307 times in 4,993 trap-nights. Captures included 375 Heermann's kangaroo rats (D. heermanni), 190 short-nosed kangaroo rats, 75 San Joaquin antelope squirrels, 51 deer mice (Peromyscus maniculatus), 19 southern grasshopper mice (Onychomys torridus), seven San Joaquin pocket mice (Perognathus inornatus), and 1 giant kangaroo rat (D. ingens).

For all species combined, mean capture rate was highest on North-Hilly sites (Table 2), but did not differ significantly among regions ($F = 0.50$; 3,16 df; $P = 0.69$). Capture rates for sites ranged from 6.8 to 24.8 and were weakly correlated with percent ground cover ($r = 0.40$, 19 df, $P = 0.08$), but capture rates were not correlated with shrub density ($r = 0.12$, 19 df, $P = 0.61$).

Heermann's kangaroo rat was the most frequently captured species in all regions except South-Flat where short-nosed kangaroo rats were more abundant (Table 3). Short-nosed kangaroo rats were the second most frequently captured species on South-Hilly and North-Flat sites, but only one was captured in North-Hilly sites. All San Joaquin pocket mice and the single giant kangaroo rat were captured on South-Flat sites. Southern grasshopper mice were captured in all regions except North-Hilly. Deer mice were noticeably more abundant on North-Hilly sites, but 23 were captured on one site and accounted for almost half of all deer mice trapped during the session. San Joaquin antelope squirrels were noticeably more abundant on South-Flat sites. San Joaquin antelope squirrel, Heermann's kangaroo rat, and short-nosed kangaroo rat were the most ubiquitous species based on the number of sites on which each species was captured (Table 3).

Number of species captured (Table 3) was highest for the South-Flat region (7) and lowest for the North-Hilly region (4). Number of species captured on individual sites ranged from two to six. Mean Shannon diversity indices (Table 3) differed significantly among regions ($F = 5.84$; 3,16 df; $P < 0.01$). Mean index was highest for South-Flat sites and lowest for North-Hilly sites. Shannon diversity indices on sites did not vary with percent ground cover ($r = 0.12$, 19 df, $P = 0.60$) or shrub density ($r = 0.02$, 19 df, $P = 0.93$).

Heermann's kangaroo rat capture rates on sites were negatively correlated with short-nosed kangaroo rat capture rates (Table 4). All other correlations were not significant.

For kangaroo rats, mean capture rate was highest in the North-Flat region (Table 5), but did not differ significantly among regions ($F = 1.48$; 3,16 df; $P = 0.26$). Kangaroo rat capture rates on individual monitoring sites were significantly correlated

with percent ground cover ($r = 0.59$, 19 df, $P < 0.01$), but were not correlated with shrub density ($r = 0.04$, 19 df, $P = 0.87$).

Although San Joaquin antelope squirrels are primarily diurnal (Best et al. 1990), sufficient numbers of squirrels were captured to permit comparisons of relative abundance. Mean capture rate for San Joaquin antelope squirrels differed significantly among regions ($F = 6.53$; 3,16 df; $P < 0.01$) and was highest on South-Flat sites and lowest on North-Flat sites (Table 5). Capture rates generally were higher on south versus north sites. San Joaquin antelope squirrel capture rates on individual sites were negatively correlated with percent ground cover ($r = -0.75$, 19 df, $P < 0.01$), but were not correlated with shrub density ($r = 0.29$, 19 df, $P = 0.21$).

Mean capture rate for short-nosed kangaroo rats differed significantly among regions ($F = 3.97$; 3,16 df; $P = 0.03$) and was highest on South-Flat sites (Table 5). Capture rates generally were higher in flat versus hilly terrain. Short-nosed kangaroo rat capture rates on individual sites were not significantly correlated with percent cover ($r = 0.19$, 19 df, $P < 0.42$) or shrub density ($r = 0.14$, 19 df, $P = 0.56$).

DISCUSSION

Small Mammal Abundance and Community Composition

Small mammal abundance is influenced by a number of factors including vegetation (both composition and structure), soil characteristics, and the presence and abundance of both predators and competitors (Kotler and Brown 1988, Brown and Harney 1993). At NPR-1, the influence of slope orientation and terrain type on small mammal communities was examined primarily because of data that indicated that habitat characteristics and kit fox abundance varied with these factors. However, slope orientation and terrain

likely influence small mammal communities primarily by affecting other factors, such as vegetation and soil characteristics (Brown 1975, Brown and Harney 1993). Thus, with respect to small mammals, slope orientation and terrain are probably covariates with other factors that have a more direct effect on small mammals.

At NPR-1, the lack of significant differences in total small mammal abundance among regions indicated that abundance apparently was similar across physiographic regions of the study area. However, the ranges of capture rates observed within regions indicated that total small mammal abundance varied locally within physiographic regions. Such differences between sites could not be explained by the variables examined.

The positive correlation between small mammal abundance and ground cover on individual sites may have been a function of the predominance of kangaroo rats, which were strongly correlated with ground cover. Increased cover may result in greater food availability for small mammals.

Shrub density did not appear to influence total small mammal abundance. Shrubs are more likely to affect abundance of particular species. Different small mammal foraging guilds apparently respond differently to shrubs (Brown et al. 1979). For example, bipedal heteromyids (e.g., kangaroo rats) reportedly forage more efficiently in areas of lower shrub density while small quadrupedal rodents (e.g., pocket mice, cricetids) preferentially forage near shrubs (Brown and Lieberman 1973, Rosenzweig 1973). However, at NPR-1 shrub density did not appear to influence kangaroo rat abundance which may indicate that shrubs probably influence microhabitat use more than site-specific abundance.

San Joaquin antelope squirrels, Heermann's kangaroo rats, and short-nosed kangaroo rats were the most ubiquitous species. Conversely, relatively few grasshopper mice and pocket mice were captured. Grasshopper mice may naturally occur in low densities (McCarty 1975). The low number of pocket mice was somewhat unexpected. During small mammal trapping sessions conducted in 1991-92 for another study on NPR-1, pocket mice were abundant and at times were the most frequently captured species (EG&G Energy Measurements, Inc. 1992a, 1992b). However, pocket mouse populations can fluctuate dramatically in response to environmental conditions (Brown and Harney 1993, Williams et al. 1993). Deer mice were noticeably more abundant on North-Hilly sites, and the reason for this is unclear. Finally, the single giant kangaroo rat captured may not accurately reflect the abundance of this species on NPR-1. Giant kangaroo rats are colonial and therefore have a clumped distribution in the environment (Grinnell 1932, Williams and Kilburn 1991). Trap lines were not located close to any giant kangaroo rat colonies, resulting in the low capture rate for this species.

Although small mammal abundance was similar among regions, community composition varied among regions and, to a lesser extent, individual sites. Diversity was highest on South-Flat sites where vegetation cover was lowest. Vegetation on these sites was more patchy resulting in a mosaic of vegetation and bare ground. This patchy mosaic may result in increased small mammal diversity by creating a locally high interspersions of microhabitats (Rosenzweig and Winakur 1969, Brown and Harney 1993).

The observed variation in community composition among regions and sites, and even the presence of particular species in regions or on sites, probably was influenced by species-specific

responses to varying habitat conditions among regions and sites (e.g., negative relationship between San Joaquin antelope squirrels and ground cover). However, competitive interactions between species also may have influenced species composition. In particular, kangaroo rats may exclude other species through both interference and exploitation competition (Bowers and Flanagan 1988), as well as through habitat modification (Heske et al. 1994). Where more than one kangaroo rat species is present, larger species may exclude smaller species (Congdon 1974, Bowers et al. 1987, Bowers and Flanagan 1988). At NPR-1, competitive exclusion of short-nosed kangaroo rats by Heermann's kangaroo rats may have resulted in the observed negative correlation between capture probabilities for these two species. Vanderbilt-White and White (1992) reported evidence of possible competitive exclusion of short-nosed kangaroo rats by Heermann's kangaroo rats and/or giant kangaroo rats on the nearby Carrizo Plain.

Heermann's kangaroo rats also may competitively exclude other species resulting in reduced abundance or even an absence of these species. Kelt (1988) cited several studies in which small mammal diversity was found to be low in areas where Heermann's kangaroo rats were abundant. Consistent with this, small mammal diversity on NPR-1 was lowest in the North-Hilly region where Heermann's kangaroo rats were most abundant and diversity was highest in the South-Flat region where Heermann's kangaroo rats were least abundant. Small-sized kangaroo rats also may exclude smaller quadrupedal species (Wondolleck 1978, Bowers et al. 1987), but such exclusion by short-nosed kangaroo rats was not evident on NPR-1.

Food Availability for Kit Foxes

Since 1986, small mammals have been the primary item in the diet of kit foxes at NPR-1 (EG&G Energy Measurements, Inc. unpubl.

data). However, total small mammal abundance patterns observed during this study were not consistent with spatial patterns of kit fox abundance. Kit foxes are more frequently captured in flat terrain (EG&G Energy Measurements, Inc. unpubl. data), but total small mammal abundance did not differ between flat and hilly terrain.

Kangaroo rats have been the small mammals most frequently consumed by kit foxes at NPR-1 (Scrivner et al. 1987). Laughrin (1970) suggested that kit foxes might even be specialized for foraging on kangaroo rats, and Grinnell et al. (1937) and Laughrin (1970) suggested that the distribution of San Joaquin kit foxes was strongly influenced by the availability of kangaroo rats. However, kangaroo rat abundance on NPR-1 was similar among regions and again does not explain observed kit fox abundance patterns. Other factors (e.g., other prey, competitors) apparently are more important than small mammals in determining kit fox abundance in regions.

Special Status Species

Although San Joaquin antelope squirrels were captured on all sites, abundance did vary with physiographic factors. The higher capture probabilities of antelope squirrels on southern treatments where ground cover was lower and the negative correlation with cover on individual sites indicates that this species may be more abundant in areas with sparser vegetative cover. The lack of association between antelope squirrels and shrub density is consistent with the observations of Harris and Stearns (1991).

Short-nosed kangaroo rats also were captured in all treatments, but abundance also varied with physiographic factors. Short-nosed kangaroo rats were most abundant in flat terrain, but it is not clear whether this is a function of vegetation characteristics, interspecific competition, or some other factor.

Hawbecker (1951) also observed that short-nosed kangaroo rats appeared to be more abundant on "gentle" terrain.

Data gathered on the distribution, abundance, and habitat relationships of both short-nosed kangaroo rats and San Joaquin antelope squirrels could facilitate the conservation of these species at NPR-1. For example, this information may be useful in identifying sensitive habitat or areas for these species. Both species appear to be abundant on NPR-1, and long-term conservation on this area in coordination with regional conservation efforts could potentially provide sufficient protection to negate the need to add these species to the Federal endangered species list.

The distribution and abundance of small mammals on NPR-1 during 1993 did not explain observed patterns of San Joaquin kit fox abundance. Other factors (e.g., availability of other prey, abundance of competitors) may be more important in determining kit fox distributional patterns. However, environmental conditions in the San Joaquin Valley are dynamic and can vary significantly with annual precipitation. Continued monitoring on NPR-1 will contribute toward understanding the effects of fluctuating environmental conditions on the abundance and distribution of small mammals on NPR-1, and the resulting effects on kit foxes.

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Table 1. Mean vegetation cover and shrub density among physiographic regions, Naval Petroleum Reserve No. 1, California, 1993.

Region	Cover (%)		Shrub Density (no./200 m ²)	
	Mean $\pm$ SE	Range	Mean $\pm$ SE	Range
South-Flat	60.1 $\pm$ 5.6 B ¹	45.5-79.5	19.8 $\pm$ 6.8 A	6-41
South-Hilly	63.7 $\pm$ 2.5 B	58.5-73.0	56.0 $\pm$ 14.5 A	28-100
North-Flat	85.2 $\pm$ 3.1 A	78.0-95.0	34.0 $\pm$ 15.1 A	3-83
North-Hilly	72.8 $\pm$ 4.9 AB	56.5-81.0	34.6 $\pm$ 14.3 A	6-88

¹ Means with the same letter within columns were not significantly different at $\alpha = 0.05$.

Table 2. Mean capture rates and Shannon diversity indices (H') for small mammals by physiographic region, Naval Petroleum Reserve No. 1, California, 1993.

Region	Individuals	Trap-nights	Capture Rate		Shannon Diversity	
			Mean $\pm$ SE	Range	Mean $\pm$ SE	Index
South-Flat	163	1,250	13.0 $\pm$ 3.1 A ¹	6.8-24.8	0.46 $\pm$ 0.05 A	0.26-0.57
South-Hilly	166	1,248	13.3 $\pm$ 1.9 A	8.4-18.9	0.40 $\pm$ 0.02 AB	0.34-0.46
North-Flat	187	1,250	15.0 $\pm$ 1.1 A	10.8-16.8	0.42 $\pm$ 0.03 A	0.34-0.50
North-Hilly	202	1,245	16.2 $\pm$ 1.8 A	11.3-21.4	0.26 $\pm$ 0.06 B	0.13-0.36

¹ Means with the same letter within columns were not significantly different.

Table 3. Number of individual small mammals captured among physiographic regions, Naval Petroleum Reserve No. 1, California, 1993.

Species	Individuals Captured				Number of sites
	South-Flat	South-Hilly	North-Flat	North-Hilly	
Short-nosed kangaroo rat	83	35	71	1	16
Heermann's kangaroo rat	19	106	99	151	19
Giant kangaroo rat	1	0	0	0	1
San Joaquin pocket mouse	7	0	0	0	2
Deer mouse	2	4	6	39	10
Southern grasshopper mouse	9	4	6	0	12
San Joaquin antelope squirrel	42	17	5	11	20

Table 4. Spearman rank correlations among capture rates for small mammal species, Naval Petroleum Reserve No. 1, California, 1993.

Species ²	Spearman rank correlations ($\underline{r}$) and $\underline{P}$ -values ¹		
	HKR	SNKR	SJAS
SNKR	-0.63 <0.01*	-	-
SJAS	-0.31 0.18	0.14 0.56	-
Quad	0.09 0.71	-0.07 0.77	-0.16 0.49

¹ * = significant at $\alpha = 0.05$.

² HKR = Heermann's kangaroo rat, SNKR = short-nosed kangaroo rat, SJAS = San Joaquin antelope squirrel, Quad = small quadrupeds (San Joaquin pocket mouse, deer mouse, and southern grasshopper mouse).

Table 5. Mean capture rates for all kangaroo rats, San Joaquin antelope squirrels, and short-nosed kangaroo rats by physiographic region, Naval Petroleum Reserve No. 1, California, 1993.

Region	Mean $\pm$ SE Capture Probability (no./100 trapnights)		
	All kangaroo rats ¹	San Joaquin antelope squirrels	Short-nosed kangaroo rats
South-Flat	8.2 $\pm$ 3.1 A ²	3.4 $\pm$ 0.8 A	6.6 $\pm$ 2.7 A
South-Hilly	11.3 $\pm$ 1.6 A	1.4 $\pm$ 0.5 AB	2.8 $\pm$ 0.9 AB
North-Flat	13.6 $\pm$ 1.1 A	0.4 $\pm$ 0.3 B	5.7 $\pm$ 0.8 AB
North-Hilly	12.2 $\pm$ 0.8 A	0.9 $\pm$ 0.4 B	0.1 $\pm$ 0.1 B

¹ Heermann's, giant, and short-nosed kangaroo rats.

² Means with the same letter within columns were not significantly different.

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